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Environmental effects on host selection and dispersal of mountain pine beetle

Mary Reid

Mountain Pine Beetle Initiative Working Paper 2007–07

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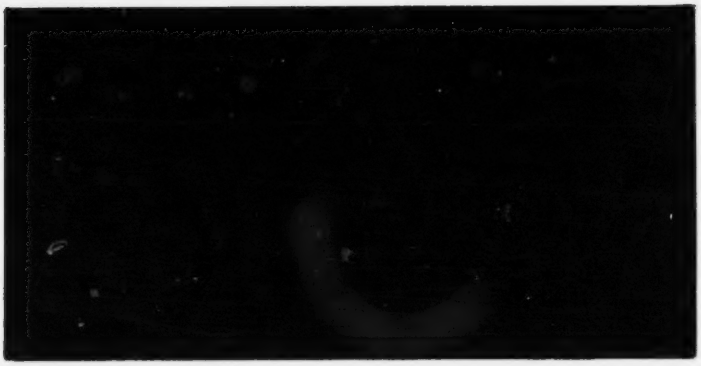

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Mountain Pine Beetle Initiative PO #4.01

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Abstract

We investigated the influence of landscape heterogeneity on processes that could influence the dispersal of mountain pine beetle, *Dendroctonus ponderosae*. Host tree quality, as measured by tree diameter, resin production, monoterpenes and phloem thickness, did not differ greatly among stands, including sites that had been thinned or burned. Live trees in the highest burn classes produced the least resin and had the thinnest phloem, and were unattractive to single beetles placed on the trees (pioneers). Pioneers entered moderately burned trees significantly more often than less or more burned trees, but this could not be attributed to tree size, resin or phloem thickness. Naturally arriving beetles were more likely to colonize trees with higher resin production and more limonene, and did so earlier on trees with more myrcene; the probability that a pioneer beetle would recruit a mass-attack was higher with higher resin flow for larger beetles. These results suggest that constitutive tree "defences" may act as attractants. Overall, larger females and those in better condition were more likely to enter trees than were smaller beetles, despite mortality costs and relatively low prospects of recruitment.

We also examined the dispersal of beetles through a pine forest and an intensively burned forest in a mark-recapture study. The burned stand was warmer and windier than the pine stand during the beetles' midday flight period. Beetles tended to disperse further in the burned stand than in the intact stand. Movement of beetles across the landscape is likely determined more by host tree availability, in turn influencing beetle energetic condition, and less by host tree quality.

Keywords: Mountain pine beetle, *Dendroctonus ponderosae*, host tree quality, resin production, colonization, tree defences, dispersal, mass-attack

Résumé

Nous avons étudié l'influence de l'hétérogénéité du paysage sur des processus qui peuvent influer sur la dispersion du dendroctone du pin ponderosa, le *Dendroctonus ponderosae*. La qualité de l'arbre hôte, que l'on mesure par le diamètre de l'arbre, par sa production de résine, par la présence de monoterpènes et par l'épaisseur du phloème, n'était pas très différente d'un peuplement à un autre, y compris dans les peuplements qui avaient été éclaircis ou brûlés. Les arbres vivants des classes les plus brûlées produisaient le moins de résine et avaient le plus mince phloème, et on a constaté qu'ils n'attiraient pas les dendroctones isolés placés sur les arbres (pionniers). Les pionniers entraient dans les arbres modérément brûlés bien plus fréquemment que dans les arbres très brûlés ou peu brûlés, mais cela ne pouvait pas être attribué à la taille de l'arbre, à sa résine ou à l'épaisseur de son phloème. Les dendroctones arrivés naturellement étaient plus susceptibles de coloniser les arbres dont la production de résine et de limonène était plus importante, et c'était le cas pour les arbres qui produisaient plus de myrcène. La probabilité qu'un pionnier recrute une attaque de masse augmentait avec le débit de résine pour les plus gros dendroctones. Ces résultats laissent à penser que les « défenses » constitutives des arbres pourraient agir comme attractifs. Globalement, les plus grosses femelles et celles en meilleure forme étaient plus susceptibles d'entrer que les dendroctones plus petits, malgré les coûts de mortalité et les espoirs relativement faibles de recrutement.

Nous avons également étudié la dispersion des dendoctrones dans une forêt de pins et dans une forêt très brûlée dans le cadre d'une étude de marquage-recapture. Le peuplement brûlé était plus chaud et plus venteux que le peuplement de pins pendant la période de vol à la mi-journée des dendroctones. Les ravageurs avaient tendance à se disperser davantage dans le peuplement brûlé que dans le peuplement intact. Le déplacement des dendroctones dans le paysage pourrait être déterminé par la disponibilité de l'arbre hôte, qui influence la situation énergétique du dendroctone, plutôt que par la qualité de l'arbre hôte.

Mots-clés : dendroctone du pin ponderosa, *Dendroctonus ponderosae*, qualité de l'arbre hôte, production de résine, colonisation, défenses de l'arbre, dispersion, attaque de masse

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Introduction

Dispersal is thought to be a key process in determining mountain pine beetles' (*Dendroctonus ponderosae*) distribution across a landscape. To prevent further widespread epidemics of mountain pine beetle, large-scale manipulations of forest structure are being proposed and implemented to diminish potential for infestation to expand. These manipulations include prescribed fire and thinning and changes in stand structure, all of which entail large economic and ecological consequences. However, we currently have little basis for predicting the consequences for beetle infestations, as our understanding of mountain pine beetle dispersal is limited.

Host tree quality is one of the factors that should influence how far these beetles move across a landscape. Pines have both physical and chemical defences in the form of resin and monoterpenes, among other secondary compounds. Before beetles attack a tree, defences are at constitutive levels. These defences may influence the probability that a tree is colonized by beetles and the success of the pioneering beetle in recruiting conspecifics to overwhelm the tree's defences. These may, in turn, influence the likelihood of beetles settling in a stand or passing through it. In addition to constitutive defences, attack by mountain pine beetle can induce defence responses in pines.

The response of a beetle to pine defences may also depend on the beetle's condition. Beetles in better condition (larger size or more energy reserves) may be better able to tolerate tree defences than can beetles in poor condition (Gries et al. 1990). This greater tolerance might predict that beetles in better condition are more likely to pioneer attacks on trees before the tree's defences are depleted by mass-attack. However, if pioneering is a net cost, through higher mortality or decreased reproduction, then beetles in better condition may choose to continue searching for a tree already under attack rather than pioneer an aggregation. In that case, beetles in poorer condition, with little ability for continued search, may be the ones that settle for pioneering attacks.

The condition of beetles is determined in part by natal habitat, but energy reserves are also depleted during dispersal. Stand structure may influence the movement of beetles through tree density that influences both the tortuosity of the flight path (Byers 1996) and the microclimate that, in turn, determines the integrity of pheromone plumes. Host tree density can influence the number of stops beetles make as they move through a stand. Energy loss during dispersal can influence subsequent reproduction (Elkin and Reid 2005) and the ability to cope with tree defences (see above).

This report summarizes our results to date on the landscape variation in lodgepole pine constitutive defences—primarily measured as resin production, but also as phloem monoterpene concentration. The response of pioneer mountain pine beetles to those defences is reviewed, measured by experimentally placing beetles on trees and by attacks of free-flying beetles, and effects of beetle quality (size, condition) on the beetles' responses are also examined. Finally, results from the study on the dispersal of mountain pine beetles through a mature lodgepole pine stand and a burned stand are presented.

Material and Methods

Several different studies were undertaken that examined tree defences and mountain pine beetles' response to those defences. Their results on shared processes are synthesized here. In brief, these studies include: 1) effect of thinning on resin defences; 2) effects of sublethal burn on resin defences and the attack response of experimental pioneer beetles; 3) the effects of constitutive resin and monoterpenes on the probability and timing of attack of mountain pine

beetles on apparently undamaged trees in intact stands, and; 4) the fitness consequences of attack by pioneer beetles as a function of their condition and of the condition of host trees.

Study sites

Our research was conducted primarily in Banff National Park, with some study sites occurring in Kootenay National Park.

To examine the effects of thinning on tree defences, we selected three sites in Banff in 2004 that had adjacent thinned and unthinned stands. The Carrot Creek site was thinned in 2003, the Boundary site was thinned in 2002, and the Tunnel Mountain site was thinned starting in February 2002. Thinned stands had from 95 to 541 stems/ha and unthinned stands had from 732 to 2260 stems/ha. We randomly sampled 30 trees in each site, and recorded tree size (diameter at breast height) and resin defences (see below).

To examine the effect of sublethal fire damage on tree defences, we chose five stands in 2004 and four stands in 2005. In the burned stands (all burned in 2003), we chose 10 trees belonging to one of five burn classes (Table 1). For comparison to the burned stands in 2005, we examined five unburned stands that shared the same aspect (180° to 250°), slope (<15°), elevation (1400 m to 1550 m) and species composition (pine dominated). Other studies of the interaction between beetles and trees were conducted in undisturbed stands of mature lodgepole pine.

Table 1. Description of burn classes for individual trees.

Burn Class	Description
0	No signs of burn above ground
1	Only burned around duff, variable in circumference and intensity
2	Burned below ~1 m on trees. Not burned through bark. If above 1 m, scales lightly blackened and not burned above 1.5 m
3	Burned above 1m, often above 2 m. Scales heavily blackened above 1 m. Bark is never burned all the way through.
4	Burned heavily well above 1m (often up to 5–8 m). Bark burned through on at least part of the tree. Variable in circumference.

Tree quality

We investigated tree defences as a function of thinning, low-intensity fire, and in unmanipulated stands. Resin was measured by drilling 5-mm diameter holes 1 cm into the tree and inserting a 2-mL pipette at a slight upward angle. Two or three pipettes were inserted 5 cm apart into each tree at the same time on the north side of the tree. The amount of resin in each tube was measured after 24 h.

Monoterpenes in phloem were sampled by removing a 2 x 5-cm piece of phloem and placing it immediately on dry ice. Samples were returned to the lab on dry ice and stored in a –70 ° C freezer until analysis. Phloem was ground by mortar and pestle under liquid nitrogen and placed into 2 ml of hexane with decane as an internal standard to extract the monoterpenes over four days. After four days, the hexane was decanted and stored at –70 ° C until analysis by gas chromatography. The monoterpenes myrcene, α-pinene, β-pinene, camphene and limonene were analyzed by comparison with standards. β-phellandrene was identified by the size and location of the peak relative to values reported in the literature. Extracted phloem was dried and weighed, and concentrations of monoterpenes were expressed as milligrams of monoterpene per gram of dried phloem.

Beetle response

In order to examine how tree quality influences the propensity of beetles to enter trees, we placed single female mountain pine beetles on the north sides of trees at breast height within plastic cages covering 100 cm^2 of bark. Prior to placement on the tree, each beetle was weighed and the width of its pronotum was measured. Females were examined every 2 h on the first day to determine if they had entered the bark, and then every day for two or three days, depending on the study. In one study to determine the fate of these beetles, some beetles were starved for 5 days prior to implanting to simulate fat loss due to dispersal. These beetles were allowed to remain in the tree, and their fate (dead, established, gone) was assessed after 1 month. Whether these beetles subsequently recruited other beetles was also recorded.

Mark-recapture study

The mark-recapture study was designed to minimize number of traps while maximizing number of distances from release points in order to get a good fit to dispersal models. From the plot centre, four platforms from which beetles were released were placed 25 m away in each cardinal direction. Four 12-unit funnel traps baited with mountain pine beetle lures (PheroTech Inc., Delta, British Columbia) were placed 50 m from the plot centre in the four cardinal directions, and another four were placed 175 m from the plot centre. Beetles were reared from infested logs in tents, and were marked by being dusted with one of four colours of fluorescent powder. The beetles were released onto the platforms at midday on calm, clear days; the traps were checked daily on each of the subsequent three days. A weather station placed at the plot centre recorded temperature and wind speed and direction every 30 sec for the month of August 2005.

Two trials were conducted in 2005. One trial occurred in Banff National Park, near Johnson Lake, in a mature lodgepole pine stand. The second trial was conducted in a stand in Kootenay National Park that was intensely burned in 2003 with no live trees remaining.

The number of beetles captured as a function of distance from the release point was analyzed by fitting these data to the models of Turchin and Thoeny (1993), and Zolubas and Byers (1995).

Results and Discussion

Variation in host quality

Resin

Thinning in Banff National Park did not have a detectable effect on constitutive resin production, although a trend was noted that trees in thinned areas produced less resin than did those in unthinned areas (Figure 1; $F_{1,144}=3.87$, $p=0.051$). There were no detectable concurrent effects of site ($F_{2,144}=2.78$, $p=0.067$), diameter at breast height ($F_{1,144}=0.50$, $p>0.48$) or tree density ($F_{1,144}=2.17$, $p>0.14$). These results differ from the commonly held expectation that thinning increases resin responses (e.g., Brown et al. 1987; Ruel et al. 1998; Kolb et al. 1998), but other studies have found limited responses to thinning (e.g., Feeney et al. 1998; Baier et al. 2002). Site-specific factors, as well as time since thinning, can affect the response of trees to thinning. For this particular study site (Banff), thinning did not detectably influence constitutive defences either positively or negatively.

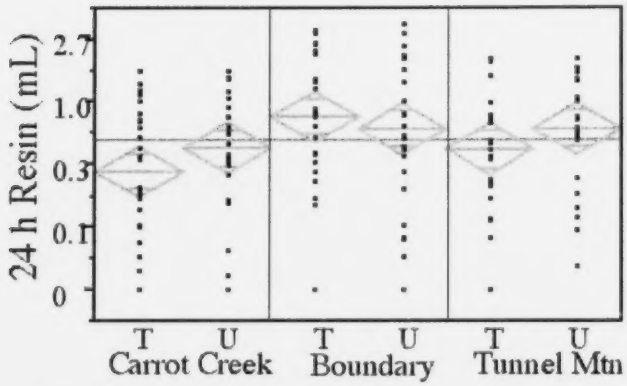

Figure 1. Resin production in three pairs of thinned (T) and unthinned (U) stands in Banff National Park. Diamonds enclose 95% CI of the mean.

Constitutive resin production tended to decline with increasing fire damage (burn class) in both 2004 and 2005 (Table 2). There was no significant difference in resin production by burned trees in the lower two burn classes (Classes 1 and 2) compared to resin production by unburned trees (Class 0), whereas resin production was significantly reduced in the higher burn classes compared to that in unburned trees in both years (Figure 2 for 2005). In 2005, when control stands with the same site characteristics as burned stands were chosen, there was no difference in resin production by trees in burned and by trees in control stands (Stand Burning, Table 2b). In contrast to these results, Santoro et al. (2000) found that resin flow tended to increase with the extent of burn on individual trees, and Feeney et al. (1998) found that trees in burned stands tended to have higher resin flows than did those in control stands. Both these studies examined resin response one and two years after thinning, as we did. There is no obvious reason for the discrepancy in results, although the studies involve different species and different sites.

Table 2. Statistical effects of burning on resin production in a) 2004, and b) 2005.

a) 2004

Effect	Df	F	p
Site	3,119	6.75	0.0003
Burn Class	3,199	10.86	<.0001
Diameter at breast height	1,199	4.85	0.03

b) 2005

Effect	Df	F	p
Stand Burning	1,239	0.18	0.68
Site [Stand Burning]	7,239	5.68	<.0001
Burn Class	4,239	8.66	<.0001
Phloem	1,239	4.26	0.04
Diameter at breast height (cm)	1,239	0.81	0.37

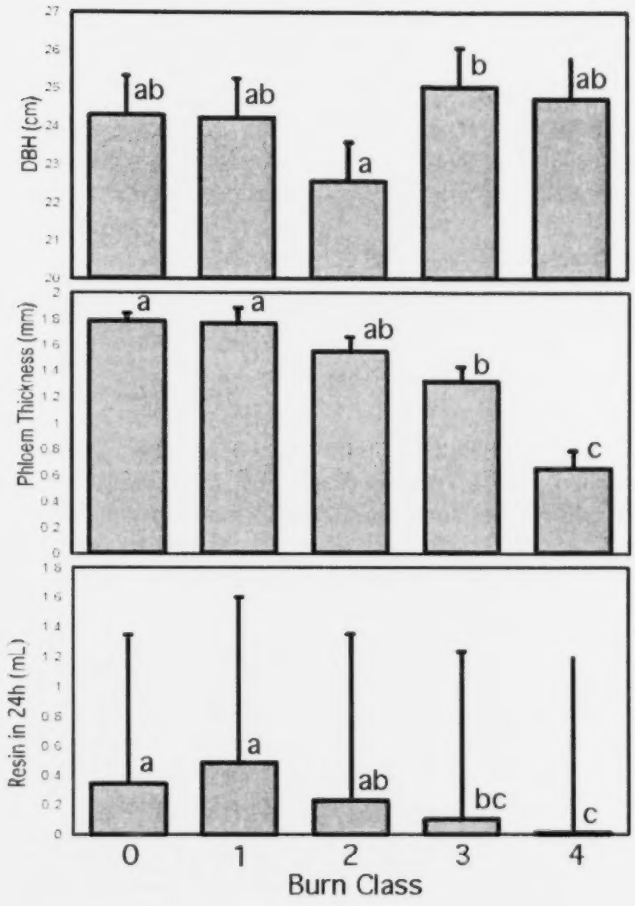

Figure 2. Tree characteristics in relation to burn class in 2005, as measured by Least Square Means (+ SE) from models reported in text.

Top panel: Diameter at breast height (DBH); middle panel: phloem thickness; bottom panel: resin produced over 24 h.

Mean and SE for diameter at breast height and resin are back-transformed from ln-transformation used in analysis. Shared letters indicate non-significant differences as determined by Tukey's HSD (Honestly Significant Differences test) on Least Square Means.

Resin response was not well explained by tree size (diameter at breast height) across several studies. In undamaged trees, in 2004, there was a weak interaction between site and diameter at breast height ($F_{4,146}$=2.55, p=0.042): one site had a positive relationship between resin and diameter at breast height ($p < 0.003$, n=41), whereas the other four sites had non-significant relationships (all $p > 0.6$, n=25 to 40). There were no detectable differences among sites ($F_{4,146}$, $p>0.75$). In burned stands in 2004, resin production increased with tree diameter (Table 2a), but in 2005, in burned and control stands, no effect of diameter at breast height on resin production was detected (Table 2b). Nebeker et al. (1995) similarly found weak effects of tree diameter on resin flow in lodgepole pine.

Phloem thickness

Phloem thickness was measured in 2005 in burned and control stands. Trees that had experienced greater fire damage had thinner phloem (Table 3, Figure 2). There was no overall difference between control and burned stands (Table 3). Phloem thickness increased with tree diameter (Table 3). There were differences in phloem thickness among stands (sites).

Table 3. Results of general linear model on phloem thickness for burned and control stands.

Effect	Df	F	p
Stand Burning	1,239	2.83	0.09
Site [Stand Burning]	7,239	2.92	0.0060
Burn Class	4,239	13.40	<.0001
Diameter at breast height (cm)	1,239	4.52	0.035
Ln(Resin+0.1) (mm)	1,239	4.26	0.040

Monoterpenes

The concentration of monoterpenes in phloem did not vary with tree size (diameter at breast height), nor were there detectable differences between the two sites sampled for monoterpenes in 2004.

Response by beetles to tree quality

The burn class of individual trees significantly influenced the proportion of beetles that entered a tree within 48 hours of being placed upon it (Figure 3; Table 4). Significantly more beetles entered trees of Burn Class 2 than they did trees of any other burn class, whereas the fewest beetles entered the most burned trees (Figure 3). Whether the stand as a whole had experienced fire did not seem to affect on the tendency of beetles to enter a tree or not.

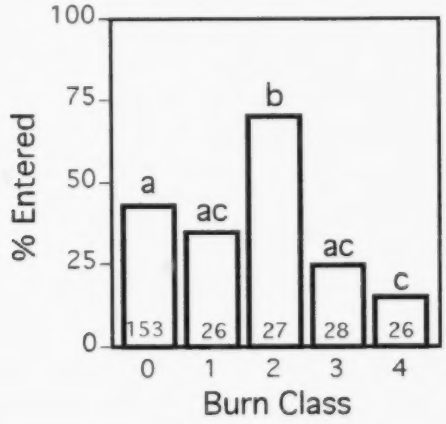

Figure 3. Percentage of beetles placed on trees that entered within 48 hours in relation to burn class, as determined univariately.

Bars that do not share letters are significantly different ($P < 0.008$). Numbers within bars are sample sizes.

Table 4. Results of logistic regression on whether a beetle entered within 48 h (n=256 beetles).

Effect	Wald $\chi 2$	p
Stand Burning	1.97	> 0.15
Site [Stand Burning]	12.91	0.0743
Burn Class	20.71	0.0004
Pronotum width (mm)	0.044	> 0.83
Body condition (mg)	5.85	0.0156

It is not clear why beetles seemed to prefer Burn Class 2. These trees did not differ significantly from trees of lower burn classes, in terms of tree diameter, resin production or phloem thickness (Figure 2). To examine this directly, we replaced "Stand Treatment" and "Burn Class" with these individual tree characteristics in a logistic regression for whether or not a beetle entered a tree within 48 h. None of the tree characteristics significantly predicted beetle entry. There was a tendency for beetles to be more likely to enter smaller trees (diameter at breast height, $p = 0.066$), as is suggested by Burn Class 2 having smaller trees (Figure 2), but this disappeared when tree characteristics were examined concurrently with stand treatment and burn class. We further

excluded Burn Classes 3 and 4 from the analyses, as the beetles were often placed on charred bark, which could obscure the other tree characteristics (Elkin and Reid 2004): even with those classes excluded, none of the tree characteristics predicted beetle entry (all $p > 0.2$).

For the beetles that did enter a tree within 48 h, Stand Treatment, Burn Class nor individual tree characteristics influenced how quickly a beetle entered at tree—whether treatment and tree characters were examined separately (Table 5) or together, or whether Burn Classes 3 and 4 were included or excluded.

Table 5. Results of general linear model for the time taken to enter a tree for those beetles that entered within 48 h.

Effect	Df	F	p
Main treatments	1,102	3.19	0.077
Site [Main treatments]	7, 102	2.58	0.017
Burn Class	4, 102	0.41	0.800
Weight-Width Residual	1, 102	0.16	0.686
Pronotum Width (mm)	1, 102	11.38	0.001

The greater propensity of mountain pine beetles to attack (moderately) fire-damaged trees rather than unburned trees has been observed in other bark beetle species (Santoro et al. 2000; Bradley and Tueller 2001), but not in mountain pine beetles attacking experimentally burned trees (Elkin and Reid 2004). Of note is that these studies observed beetles naturally recruiting to trees, whereas our study tested beetle response by placing single beetles on trees. In low populations, the success of mountain pine beetles that naturally attacked trees that had been experimentally burned tended to be higher than controls for slightly and completely burned trees, but lower for partly burned trees (Elkin and Reid 2004). This may be reconciled with the current study if beetles attacking moderately burned trees (Class 2) were likely to have greater success corresponding to the slightly burned category in Elkin and Reid (2004). The aversion to the most burned trees in the current study may be related to the aversion to charred bark observed by Elkin and Reid (2004).

Regarding pioneer beetles placed on unattacked trees in unburned stands, we examined their subsequent survival and whether they successfully recruited conspecifics. Overall (across two years and in both Banff and Kootenay National Parks), 19% of 199 beetles died after attempting to enter. There was a tendency (not significant: $p = 0.068$), when tree age was also considered, for mortality to be higher when resin was higher. The probability that a pioneer beetle successfully recruited conspecifics (a mass attack) depended on an interaction between beetle size and tree resin production ($p = 0.044$). Small beetles were less successful at recruiting when resin production was greater, whereas large beetles were more successful when resin was greater.

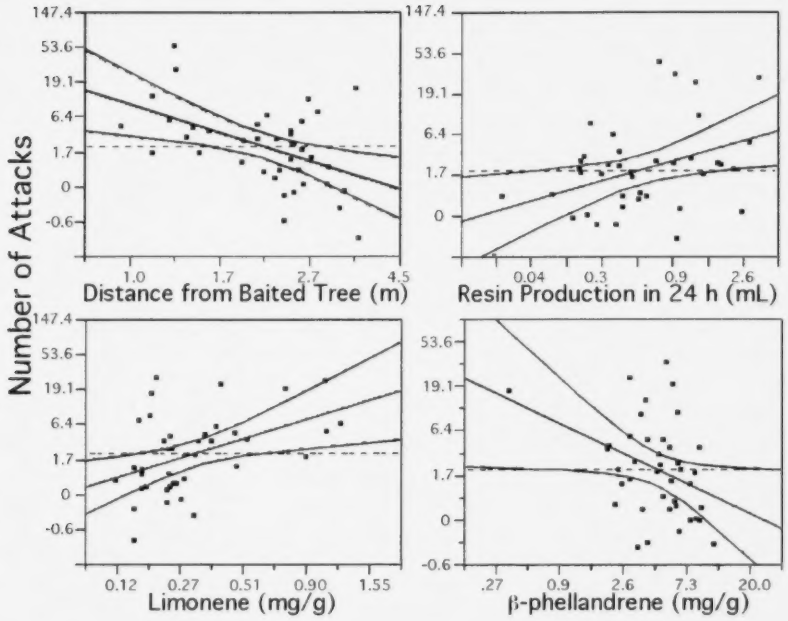

Figure 4. Leverage plots for the significant effects on the number of mountain pine beetle attacks on focal [neighbour] trees.

Axis values have been back-transformed. The original transformations were ln(number of attacks +1), ln(distance), ln(resin + 0.1), ln(limonene + 0.1), ln(β-phellandrene + 0.1).

When voluntary attacks are considered on undamaged trees near baited trees (n = 39), it appeared that trees with more constitutive resin ($p = 0.02$) and higher limonene concentrations in phloem ($p = 0.01$) were more likely to be attacked (Figure 4). Trees with lower β-phellandrene tended to have more attacks ($p = 0.04$). Trees closer to baited trees were more likely to be attacked ($p = 0.005$), but there was no effect of tree diameter, α-pinene, β-pinene or myrcene (all $p > 0.4$). We analyzed these data using the number of beetles attacking trees, but the results were similar when we considered only whether or not a tree was attacked at all. Of the trees that were attacked, those with higher constitutive myrcene concentrations in phloem were attacked sooner than those with less myrcene (Figure 5; $p = 0.03$, n=18 trees). The date at which the baited tree was attacked was positively related to the date whenthe neighbour was attacked ($p = 0.0018$), but distance to the baited tree, tree diameter, constitutive resin and other monoterpenes did not influence the date of attack (all $p > 0.1$).

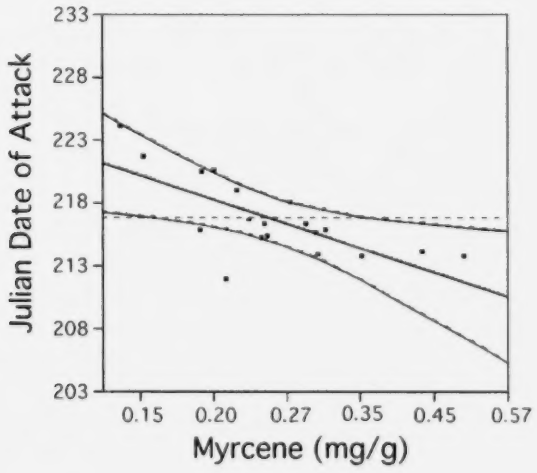

Figure 5. Leverage plot for the effect of myrcene concentration in phloem (mg myrcene/g dried phloem) on the Julian date of attack for those focal trees that were attacked (July 22 = 203).

These results suggest that trees with higher constitutive defences (resin and some monoterpenes) may be more attractive to mountain pine beetles than are trees with lower defences. In this case, these compounds would be better described as attractants than as defences. Constitutive "defences", which are much lower than induced defences (Raffa and Smalley 1995), may be attractive because they are correlated with thicker phloem (Table 3), which in turn positively affects reproductive success. Higher concentrations of monoterpenes that are pheromone precursors may enhance pheromone production (Byers et al. 1979) and thus recruitment success, although we did not detect an effect of α-pinene that is a precursor to a mountain pine beetle pheromone. In experiments using artificial pheromone lures, beetle attraction to traps increases with increasing monoterpene-elease rates (Miller and Borden 2000). Mountain pine beetles may be less deterred by monoterpenes and resin than other bark beetle species are, because mountain pine beetles specialize on live trees with a mass-attack behaviour than can overcome tree defences. Among spruce beetles (*Dendroctonus rufipennis*), individuals in epidemic population stages were less averse to monoterpenes than were those in endemic populations (Wallin and Raffa 2004), and Sturgeon (1979) observed that populations of ponderosa pine that had experienced outbreaks of western pine beetle (*D. brevicomis*) had lower α-pinene concentrations in resin than had populations that had outbreaks, suggesting that these beetles were choosing trees with higher α-pinene concentrations. Together, these observations suggest that resin and monoterpenes, at least at constitutive levels, may be attractive cues for aggressive species of bark beetles.

Effect of beetle quality

Beetle size and condition had significant effects on beetles' propensity to enter trees, as seen in two of our studies. In the burn study, beetles in better condition were more likely to enter trees than were beetles in poorer condition (Table 4, Figure 6). Of the beetles that entered, larger beetles entered more quickly than did smaller beetles (Table 5, Figure 7). A separate study also found that beetles in better condition are more likely to enter a tree ($p < 0.01$, $n = 234$); however, in that study, beetles that had been starved (very poor condition) entered the tree more quickly than those that had not been. There was also an interaction with body size and resin flow, where starved beetles entered more quickly into lower resin trees, whereas unstarved beetles were unaffected by resin production.

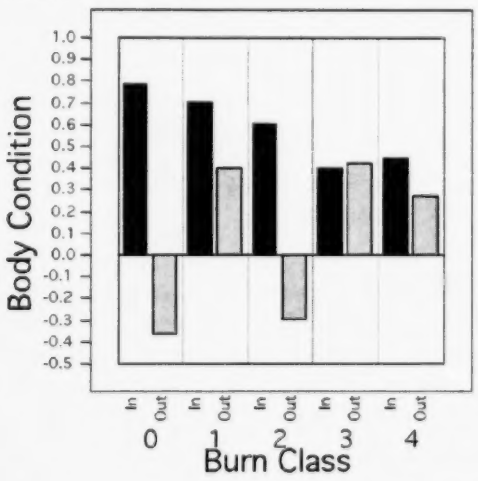

Figure 6. Body condition (residuals of weight vs. pronotum width) of beetles that entered (in) or did not enter (out) a tree within 48 h, for each burn class within burned stands.

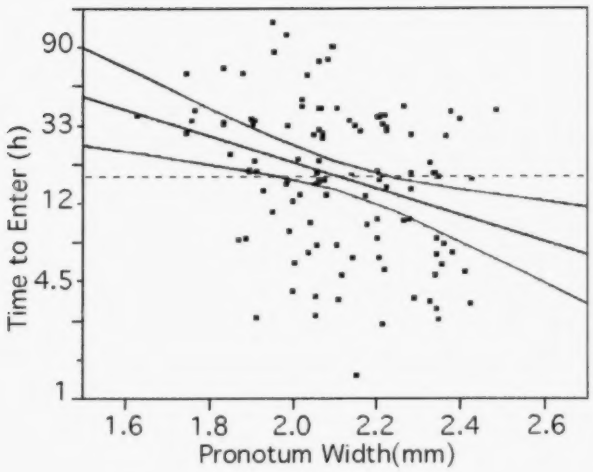

Figure 7. Leverage plot of time to enter as a function of pronotum width from model of time to enter by beetles that entered within 48 h.

Solid lines indicate regression and confidence interval; horizontal dashed line indicates grand mean

These results indicate that beetles that are larger or in better condition will contribute more to the expansion of mountain pine beetle populations because they are more willing and able to colonize trees as pioneers than are beetles that are smaller or in poorer condition. Pine engravers (*Ips pini*) that were in better condition have been shown to be better able to tolerate higher myrcene conditions than are those that have been starved or flight-exercised (Gries et al. 1990). Moreover, mountain pine beetles that had more energy reserves at the time of settlement had persistently larger eggs than did those that had been starved (Elkin and Reid 2005). Consequently, we would expect that beetles should choose to settle as soon as possible after leaving their natal site in order to achieve the highest choice of hosts and the greatest reproductive success.

Mark-recapture study

Microclimate

Temperature and wind data, sampled every 30 sec, were assembled into hourly averages for the month of August 2005. As expected with the more open canopy, the burned stand reached higher daytime temperatures and winds (Figure 8). Of note is that the differences were greatest in mid-afternoon when beetles are more likely to disperse.

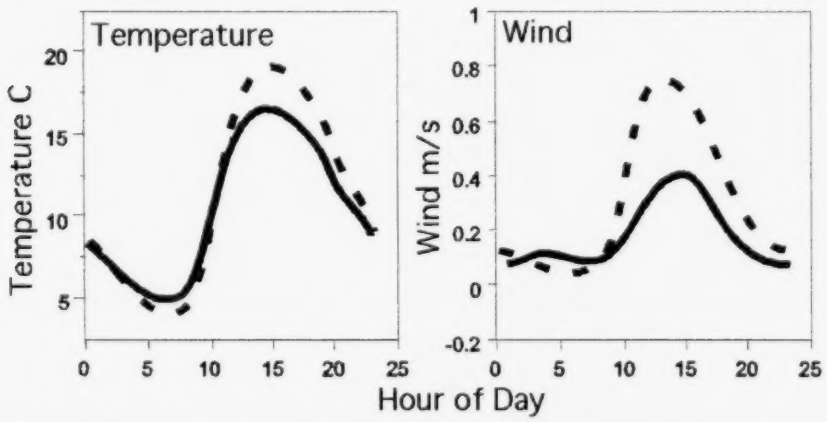

Figure 8. Diurnal temperature and wind profiles, averaged for August 2005, for a mature lodgepole pine forest (in Banff, solid line) and a burned forest (Kootenay, dashed line).

Dispersal functions

Fitted models in the two forest types suggest that beetles dispersed further in the burned stand than in the pine stand, as expected (Figure 9). Estimated mean dispersal distances, derived from the fitted diffusion model of Turchin and Thoeny (1993), were 356 m and 303 m for burned and pine stands, respectively. Fitted parameters using Zolubas and Byers (1995) area-ratio model for the same data indicate that trap effectiveness for the two stands were similar, but that the attraction radius was greater in the pine stand (75 m) than in the burned stand (56 m). The smaller attraction radius for the burned stand may be because pheromone plumes are more disrupted in the warmer and windier burned stand than in the pine stand.

The limited replication of this study means interpretations should be made with caution. However, the results are in the expected direction. Dispersal distances tended to be higher in the burned stand than in the pine stand, which is simultaneously consistent with disrupted pheromone plumes due to higher wind and temperatures in more open canopied forests, less clutter from understorey trees and shrubs to navigate around, and fewer host trees to investigate. Future research will probe these factors to determine mountain pine beetle dispersal.

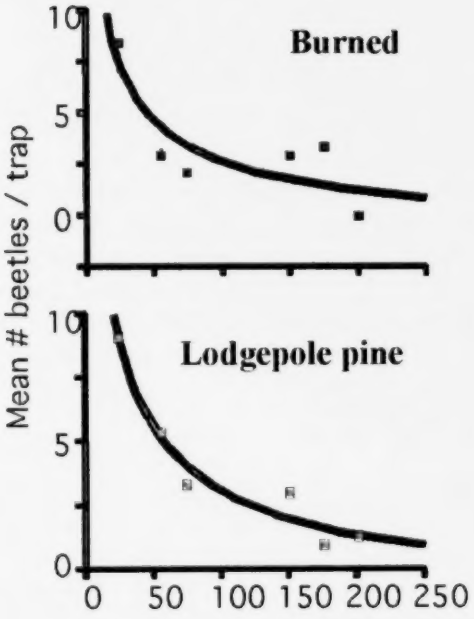

Figure 9. Distribution of recaptured marked beetles with fitted curves from the dispersal model of Turchin and Thoeny (1993).

Conclusions

Host tree quality, as measured by tree size, defences, and phloem thickness, did not differ greatly among stands—including even those stands that had been subjected to thinning and burning. When experimentally placed on these trees in thinned or burned stand, mountain pine beetles entered trees with moderate fire damage more often than they did tress with either no damage or significant damage. However, an overall increase in activity in burned stands is not likely to occur, because the apparent enhancement of tree susceptibility will be balanced by the reduced likelihood of attack of more heavily damaged trees. With the caveat that these results reflect a short window of time, and shortly after disturbance for thinning and burning, it appears that

landscape variation in tree characteristics thought to be pertinent to mountain pine beetles may not be great and need not constrain management approaches.

At the individual tree level, there was evidence that trees with higher constitutive 'defences' may be more attractive to mountain pine beetles, contrary to conventional wisdom. This conclusion needs further substantiation, but it should be considered if there are plans to select for lodgepole pine trees with higher 'defences' to replant across the landscape.

The quality of individual beetles, as measured by body size and energetic condition, was an important predictor of beetle's propensity to enter trees and their success in recruiting conspecifics to mass-attack. One implication of this is that we would expect beetles to limit dispersal flight if possible, so this may constrain long-distance dispersal. Another is that landscapes that increase the cost of dispersal might significantly reduce the rate of spread of mountain pine beetles. Our mark-recapture study suggested that beetles move farther in stands without hosts and that are more open—which could simultaneously increase the distance of spread but decrease the energetic reserves of beetles. The net effect of landscape heterogeneity on the spread of mountain pine beetles needs further investigation.

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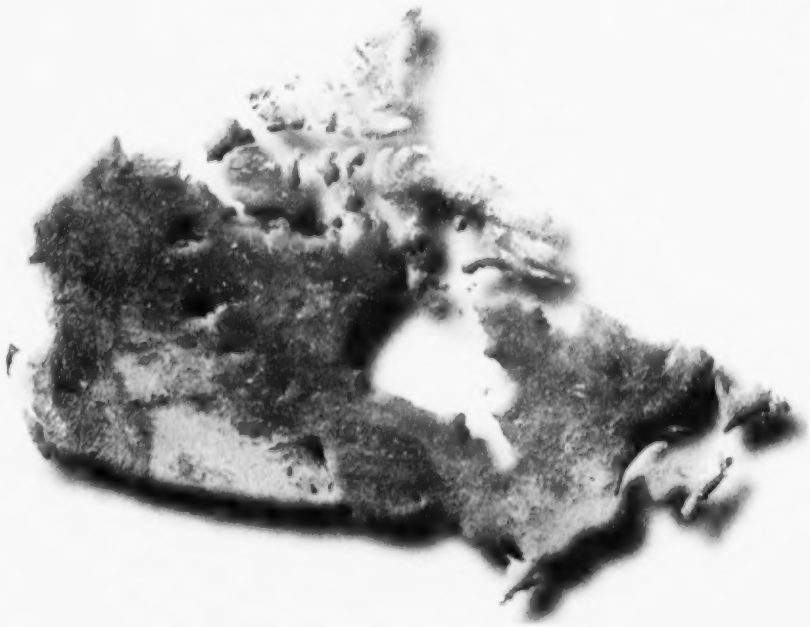

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